SPATIAL AND TEMPORAL PATTERNS IN RECRUITMENT FOR AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN THE NORTHWESTERN ATLANTIC

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The lobster, *Homarus americanus*, is a long-lived crustacean that has been heavily exploited along the northeast coast of North America for over 100 years. Catches revived markedly in many lobster fisheries during the 1980s after prolonged declines from peaks at the turn of this century. Because of high exploitation rates, the increased yields are assumed to reflect real changes in lobster abundance, although there is no consensus on why recruitment should have improved. Geographic comparisons of time series of landings, larval surveys and oceanography have indicated tentative stock boundaries but there is little understanding of stock-recruitment relationships. To-date, none of the numerous biotic and abiotic factors that have been hypothesized as controlling lobster recruitment have proven reliable for forecasting yields. Work on the behavioural ecology of the cryptic early benthic stages has invoked various density-dependent mechanisms as population controls in local areas; however, these mechanisms may not account for larger-scale recruitment events. Changes in climate, and to a lesser extent, reduced exploitation rates in the last 20 years may have caused a general increase in recruitment, producing yields to match historic highs in some lobster fisheries. There are implications for both traditional fisheries models and management if lobster stocks are dominated by 'supply-side' recruitment dynamics under the control of an unpredictable climatic phenomenon. ☐ *Lobster, life history, fishery, density-dependence, recruitment mechanisms, research approach.*

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The American lobster, *Homarus americanus*, is the largest and most abundant species of 'true' or clawed lobster (Nephropoidea). Some specimens have been reported to achieve a live weight over 19 kg (Wolff, 1978). The species has a largely boreal distribution along the northeastern coast of North America, from the Strait of Belle Isle through the Gulf of St. Lawrence, and the Gulf of Maine to Wilmington, North Carolina (Williams, 1984). The Gulf Stream around Cape Hatteras, North Carolina appears to present a thermal barrier at the southern limit (Fig. 1). The total range of the species extends over 15 degrees of latitude. Lobster (Note: throughout the text lobster refers to the American lobster, *H. americanus*, unless indicated otherwise) usually occur within 20–25 km of the coast at depths shallower than 50 m; however, populations exist on the continental shelf and offshore banks, extending to depths of over 700 m in the canyons of the continental slope.

Before commercial exploitation began, American lobster was common even in intertidal areas and collected for food by Indians and, later by the early European settlers. Lobster was so abundant it was reportedly used for agricultural fertilizer (DeWolf, 1974). Lobster fisheries have been of major economic and cultural importance for over one hundred years. Commercial harvesting started in Massachusetts in the early 1800s and had reached Maine by 1840 (Herrick, 1911). Lobster fishing in Canadian waters expanded rapidly after the introduction of canneries to Nova Scotia in 1851. Lobster landings began in Quebec in 1871, Newfoundland in 1874 and the Magdelen Islands in 1875; the Canadian fishery was considered to be fully developed by the 1890s (Robinson, 1980; Pringle *et al.*, 1983). Monitoring and regulation of the various lobster fisheries began as early as 1873, biological research soon after (Herrick, 1896). Although American lobster appears one of

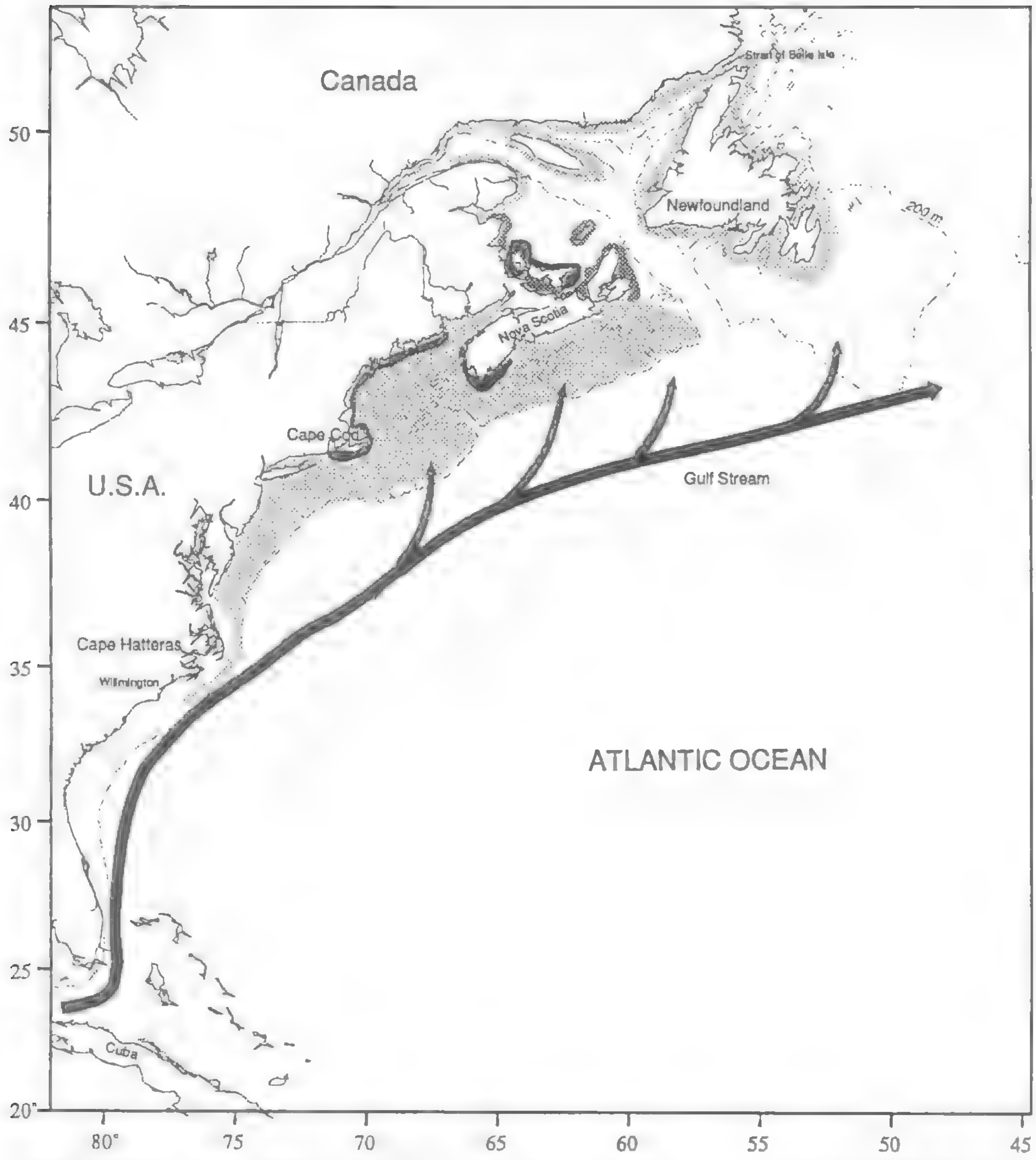

FIG. 1. The geographical distribution of American lobster, *Homarus americanus* (shaded) along the coast of North America; note, major fishing areas (black).

the most intensively studied and popularly recognized marine crustaceans there remain large gaps in understanding of its life history and the ecological mechanisms controlling abundance. Consequently, powers to predict recruitment are limited, and determining the consequences of fisheries management initiatives is problematic. The present paper reviews the biological basis to recruitment, the development of the commercial fishery and postulated recruitment mechanisms. Progress in describing lobster life history dynamics and understanding the factors that influence recruitment patterns is argued to have been hindered by the lack of an effective postlarval collector, long-term data sets on oceanographic events and the overall scientific approach.

BIOLOGICAL BASIS TO RECRUITMENT

A female lobster carries between 7,000 to 97,000 eggs, depending on body size and origin, on her abdominal pleopods for 9–12 months. Brooding time is strongly related to temperature (Templeman, 1940a; Perkins, 1972). Ovigerous females undertake seasonal depth migrations that appear associated with maximizing degree days needed for egg development: hatching eggs in relatively shallow, warm water increases survivorship of larvae by decreasing development time to the benthic stage (Campbell, 1986a, 1990a; Campbell and Stasko, 1986). The eggs hatch during summer (July – September) and the four stages of free-living pelagic larvae remain in the water column for 1–2 months, depending on temperature (Templeman, 1940b). Stage IV larvae become benthic in late summer, settling into preferred substrates such as gravel (Cobb, 1971, 1977; Cobb *et al.*, 1983,1989). Mortality during the larval stages is probably high, due to predators, starvation and physical factors (Scarratt, 1964, 1973; Caddy, 1979; Harding *et al.*, 1982). Early postlarvae are cryptic and burrow into preferred substrates where they are less susceptible to predation and may filter feed (Pottle and Elner, 1982; Lavalli and Barshaw, 1986, 1989; Barshaw and Lavalli, 1988). There is uncertainty whether the few inshore settlement sites that have been discovered should be considered 'nurseries' (areas preferentially selected for settlement) *per se* or merely areas with appropriate bottom characteristics where postlarval survival and, hence, density, is higher than other settlement sites. Lobster above approximately 40 mm carapace length (C.L.) frequently forage outside their burrows, roaming progressively further afield as they become larger and mature (Lawton, 1987). However, substrate characteristics, particularly size and availability of shelters, continues to strongly influence lobster distribution and abundance (Scarratt, 1968; Cobb, 1971; Cobb *et al.*, 1986; Hudon, 1987).

Recruitment-related variables such as growth rate, size at maturity and spawning characteristics vary with environmental conditions, notably temperature (Aiken and Waddy, 1986). Lobster attain the current legal minimum size, for most grounds around Nova Scotia, of 81 mm C.L. after five to eight years. In some areas, such as the Gulf of St. Lawrence, 'canner' lobsters of 64 mm C.L. are fished and recruitment into the fishery may occur at an even earlier age. In addition, summer temperatures over much of the southern Gulf of St. Lawrence may be sufficiently high to permit two moults per year, instead of the usual one, for newly recruited lobster. Offshore lobster also grow relatively fast, attaining fishable size after 4–5 years, as compared to the 7–12 years required for those on some nearshore grounds (Cooper, 1977). Most lobster reach fishable size before attaining sexual maturity (Ennis, 1986; Cobb and Wang, 1985). Although tagging and laboratory studies have provided extensive information on moulting and growth for immature and early adult stages (Miller *et al.*, 1989), estimating the age of older adults is problematic, as the intermoult period becomes longer and less predictable after the onset of maturity. Aging is further complicated because mature females can delay moulting in order to extrude a further batch of eggs (Waddy and Aiken, 1986).

There is no consensus on the natural life-span for lobster. Cooper and Uzmann (1977) computed a von Bertalanffy growth equation, using L_α values of 270 mm C.L. (males) and 240 mm C.L. (females), that provided maximum estimates of 100 years for offshore specimens. Estimates by Campbell (1983a) suggest more rapid growth whereby males and females reach 200 mm C.L. in 20 and 30 years, respectively.

For American lobster, as for most marine invertebrates, critical linkages between oceanography and larval life-history phases are lacking, and the existence of a stock-recruitment relationship is largely a matter of faith (Cobb and Wang, 1985). Sources of recruitment and larval mixing are only superficially understood, and consequently so are mechanisms for variability in recruitment patterns. Development of predictive models has been slow. Studies in the Northumberland Strait (Scarratt 1964, 1973) have failed to demonstrate a correlation between abundance of stage I lobster larvae and the parent stock or a predictive relationship between the production of stage IV larvae and subsequent recruitment into the fishery (but see Fogarty and Idoine (1986) for a re-evaluation). However, Campbell (1990b) derived a prerecruit abundance index from commercial traps to predict recruitment for lobster grounds off southwestern Nova Scotia 1–2 years later.

For the purposes of this paper, a stock is defined as 'a population of organisms which, sharing a common gene pool, is sufficiently distinct to warrant consideration as a self-perpetuating system that can be managed' (Larkin, 1972). We define recruitment broadly as survival from some earlier life-history stage to the minimum legal size for the commercial fishery. The continuity of the stock in time and space depends on the larvae or a later life-history phase returning to the brood area to complete the genetic cycle. Egg hatching locations are often far from habitats favorable to juveniles, which, in turn, may differ from areas preferred by adults. If a species has not evolved a reproductive strategy that returns recruits to the fishing grounds regularly, the stability of the stock cannot be assumed and it will be practically impossible to predict recruitment.

The delineation of stocks and the mechanics of stock-recruitment relationships are problems fundamental to fisheries science. Presumably if stocks can be identified, effective management regimes can be imposed to optimise exploitation of the resource. Ennis (1986) detailed five requirements for determining a stock-recruitment relationship:

1. a population that is more or less discrete, both geographically and biologically (i.e. a stock);
2. measure of stock size over a time period when abundance ranged widely;
3. measure of recruitment to the stock which coincides with the same time period;
4. understanding of the effect of variation in factors other than stock size on recruitment variability; and,
5. understanding of recruitment processes for the stock.

Although components of all five have been studied for *H. americanus* there has been no concerted attempt to integrate results and re-define management areas. Campbell and Mohn (1983) examined historical catch data from the Canadian Maritime Provinces and Maine and defined broad geographic population boundaries for lobster on the basis of coherence in temporal trends in landings over several decades. A similar exercise performed by Harding *et al.* (1983) suggested the same major groupings. Although morphometric studies have indicated some segregation of inshore and offshore lobster (Saila and Flowers, 1969) the movement patterns of mature lobster and the propensity for larval exchange suggest that genetic mixing occurs at least within the Gulf of Maine system (Campbell and Stasko, 1985, 1986). To date, attempts to delineate lobster stocks on the basis of parasites (Uzmann, 1970; Boghen, 1978; Stewart, 1980; Brattey and Campbell, 1986) have had only limited success. Protein electrophoresis indicates that American lobster from various areas are genetically similar, with the exception of a single enzyme that allows discrimination between lobsters from Prince Edward Island and south of Cape Cod (Tracey *et al.*, 1975).

Mark-recapture studies in Canada (Miller *et al.*, 1989) have shown that while immature commercial-sized lobster travel only short distances (Campbell, 1982), mature lobsters undertake extensive movements (> 100 km) and tend to return to the location where they were initially marked (Pezzack and Duggan, 1986; Campbell, 1986a). This homing behaviour may involve a round trip movement of up to 400 km in one year (Campbell, 1989). In addition, short, seasonal inshore-offshore, or shallow-deep, migrations have been noted in the Gulf of Maine, on Georges Bank and off the Magdelen Islands (Saila and Flowers, 1968; Dow, 1974; Cooper and Uzmann, 1980; Krouse, 1980; Campbell and Stasko, 1986). The movements appear associated with maintaining maximum local temperatures (Cooper and Uzmann, 1971; Campbell and Stasko, 1986). In comparison, tagging studies off eastern Nova Scotia, around Newfoundland and, generally, in the Gulf of St. Lawrence have revealed only small-scale movements (< 15 km) (Ennis, 1984).

Movement patterns for lobster larvae are poorly known and investigators have usually related larval pathways to residual surface currents. Various attempts have been made to elucidate larval sources for the Nova Scotian Atlantic coast and the rich inshore fishing grounds off southwestern Nova Scotia. While Stasko (1978) hypothesised that Browns Bank was the source of larvae for southwestern Nova Scotia, Harding *et al.* (1983) suggested the larvae originate from Georges Bank (but see also Harding and Trites, 1988, 1989; Pezzack, 1989). Dadswell (1979), on the assumption that circular currents retain larvae within an area while longitudinal currents carry larvae away, proposed that there are six lobster-recruitment cells for the Canadian Maritimes. More recent work has shown that lobster larvae exhibit pronounced diurnal vertical migration behaviour and should not necessarily be considered passive surface drifters (Harding *et al.*, 1987). If lobster larvae resemble other decapod larvae, this behaviour may maintain their position (Sulkin, 1986). Lobster larvae were collected only at the surface and only with onshore winds during a study in a nearshore area off Newfoundland, also suggesting that a nearshore retention mechanism exists (Ennis, 1983).

THE FISHERY

For over 100 years, American lobster have been predominantly caught by traps, both in Canada and the U.S.A.. Prior to the late 1860s lobster were captured by a variety of methods including hooks, spears and hoop nets (DeWolf, 1974; Dow, 1980). The majority of offshore fisheries use large traps but in some offshore areas of the U.S.A. otter trawling has occasionally supplemented trapping (Dow, 1980; Fogarty *et al.*, 1982; Pezzack and Duggan, 1983). The various inshore and offshore lobster fisheries are partitioned into management areas based on socioeconomic considerations rather than biological criteria (Dow, 1980; Pringle *et al.*, 1983; Campbell, 1989). Depending on the area involved, conservative management of these lobster fisheries has included a combination of regulations : minimum and maximum sizes, protection of ovigerous females, effort restrictions through license and trap limitations and season openings and closures, plus quota restrictions for the offshore fishery (Dow, 1980; Fogarty *et al.*, 1982; Pezzack and Duggan, 1983; Pringle *et al.*, 1983; Campbell, 1986b, 1989). Without adequate empirical stock-recruitment data determining whether these regulations have been effective conservation tools is impossible.

Historically, landings have fluctuated considerably (Fig. 2) but in recent years they have generally risen for most areas (Fig. 3). Total North American landings exceeded 60,000 t (Ennis, 1986) and Canadian lobster landings reached over 45,000 t per annum in the last century. Record lows in the 1960s and 1970s have been followed by all time highs in the 1980s; total Canadian lobster landings doubled between 1977 and 1986 and in some areas rose by an order of magnitude. The main reason for the rise appears to be an increase in the absolute abundance of lobster (Miller *et al.*, 1987). Although there has been some increased fishing effort and expansion to new grounds, catch rates have also increased. In addition, management measures, including more stringent enforcement of regulations and a reduction in the number of licenses, have helped sustain the recovery in Canada.

Historical fishing effort trends are not as well known as landings for the American lobster. Fishing effort can fluctuate with many factors such as market demand (Dow, 1980) and increases in fishing gear efficiency; also, trapability can vary from location to location depending on lobster activity and physiological condition (McLeese and Wilder, 1958; Elner, 1980). However, because effort is high (currently, there are about 10,000 licensed lobster vessels in Canada and exploitation rates have been estimated at

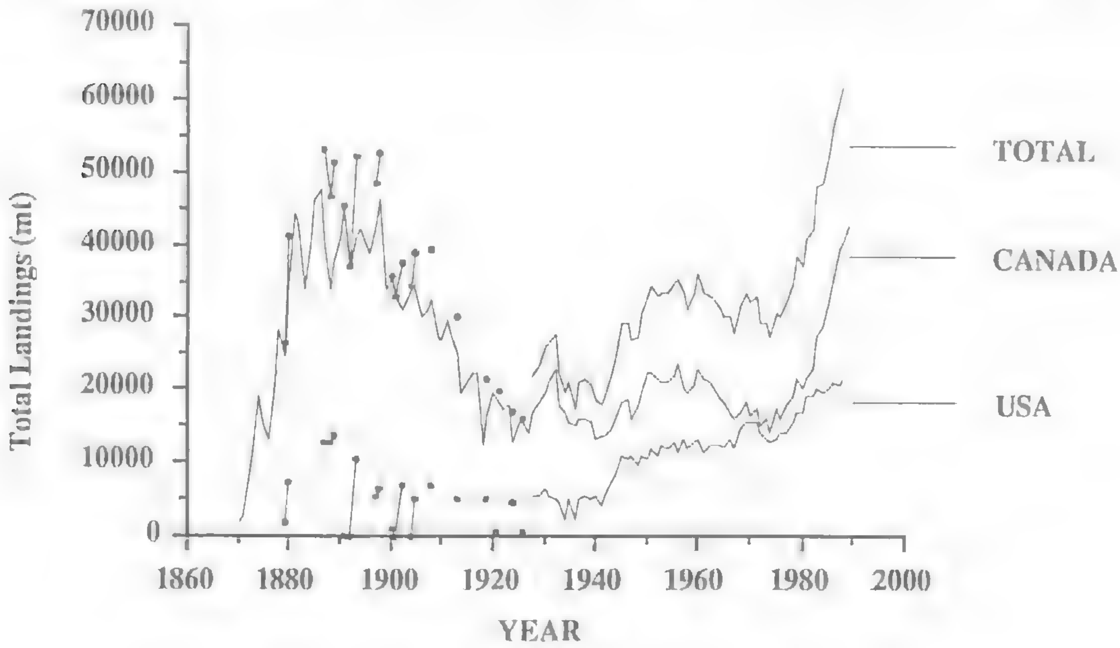

FIG. 2. Annual landings of American lobster for Canada and the U.S.A., 1870–1989.

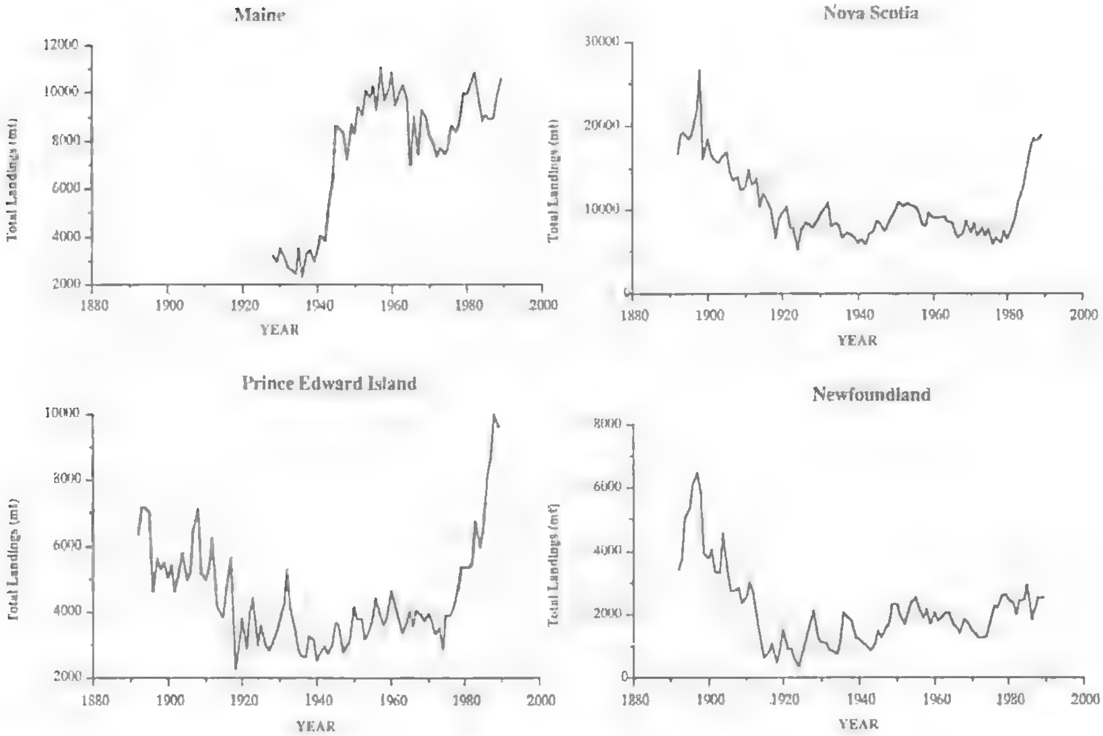

FIG. 3. Annual landings of American lobster for Maine, Nova Scotia, Prince Edward Island and Newfoundland, from the late 1880s–1989.

60–90% (Anthony, 1980; Campbell, 1980; Miller *et al.*, 1987)) catches mainly comprise lobster that are newly-recruited to commercial size and the assumption is that landings are a reliable indication of the total fishable biomass. Therefore, major fluctuations in recruitment (lobster molting into the fishery) will be reflected in the landing trends. Recent increases in exploitation of large mature lobster, an important source of recruits, concurrent with high exploitation of newly recruited lobster in the inshore fishery has caused concern that the amplitude of landing fluctuations could increase until recruitment failure occurs (Campbell, 1989).

RECRUITMENT MECHANISMS

Throughout their extensive geographical distribution American lobster are found in a diverse array of habitats, from the intertidal zone to a variety of coastal sublittoral habitats to the canyons of the continental slope (Cooper and Uzmann, 1977). Because physical and biological factors vary widely (e.g. temperature can be from 0°C to 25°C) their influence on recruitment will change in time and space (Aiken and Waddy, 1986); thus, understanding recruitment mechanisms is a challenging task. After a century of research fundamental factors such as the relationships between the seasonal movements of adult lobster, distribution of brood stock, larval recruitment processes and oceanographic features are still unclear. The numerous attempts to explain fluctuations in lobster abundance have included factors and mechanisms such as:

— Temperature variation (Flowers and Saila, 1972; Dow, 1977; Fogarty, 1988) which acts strongly to regulate activity and trapability of commercial-sized lobster (McLeese and Wilder, 1958) and the growth rates of all life-history stages. The probability of moulting is strongly temperature related and the proportion of lobster that moult can decrease by nearly 50% in cold years (Campbell, 1983b).

— Freshwater river discharge (Sutcliffe, 1973) which influences food production and, hence, larval survival. Other workers (Sheldon *et al.*, 1982) suggest that increased discharge intensifies stratification, causing higher heat retention, faster larval development and improved survival.

— Excessive exploitation rates, which reduce eggs per recruit (Robinson, 1979; Campbell and Robinson, 1983) causing recruitment failures and declines in landings. Egg predators (Campbell and Brattey, 1986; Fogarty and Idoine, 1986) and anthropogenic factors (Aiken and Waddy, 1986) have also been hypothesised as reducing eggs per recruit.

— Ecosystem productivity changes (Wharton and Mann, 1981) and competition with sea urchins for space (Garnick, 1989) which affect recruitment.

We do not intend to account for all the hypotheses that have arisen (Ennis, 1986), but rather describe the general history and progress of research to elucidate lobster recruitment patterns.

In the 1970s, during the period of collapsed lobster landings along the Atlantic coast of Nova Scotia, workers suggested several causes for the slump: recruit overfishing (Robinson, 1979), ecosystem deterioration due to a population explosion of sea urchins triggered by overfishing lobster (Wharton and Mann, 1981) and closing the Strait of Canso blocking an important source of larvae (Dadswell, 1979). Subsequently, the recruitment failure was attributed by Harding *et al.* (1983) to all three scenarios: excessive fishing of immature lobster between the 1890s and 1920 depleted the breeding stock and caused the initial decline in landings; climatic cooling and the closure of the Strait of Canso further reduced lobster stocks and, in the absence of predation by lobster, destructive grazing of macroalgal beds by sea urchins reduced the carrying capacity of the environment for lobster. None of these explanations was subjected to thorough scientific testing and each had its proponents and critics (McCracken, 1979; Pringle *et al.*, 1982; Elner and Vadas, 1990). Meanwhile, apart from reducing the number of licensed vessels, fisheries managers took little action and, from either inertia or their conservative nature, were still considering the situation when landings started to recover during the early 1980s. The sea urchins suffered mass mortality from disease and macroalgal beds recovered while landings increased (Miller and Colodey, 1983; Miller, 1985a; Scheibling and Raymond, 1990). The cause of the upturn is as enigmatic as explanations for the decline, especially with respect to the role of macroalgae. However, no reliable evidence links lobster production to macroalgae (Miller, 1985b; Elner and Campbell, 1987). Indeed, lobsters responsible for the increased landings in the early-to-mid 1980s spent their pre-recruit years during the mid-1970s on the urchin barrens. The appearance and virulence of the sea urchin pathogen in 1980 has been linked to unusually warm seawater temperatures (Scheibling and Stephenson, 1984; Miller, 1985a; Margosian *et al.*, 1987). Possibly urchin die-offs and revived lobster landings are caused by the same environmental factor(s) (Fig. 4).

The dramatic turnabout in the lobster fishery during the 1980s was a surprise given the arguments that inshore stocks should, in theory, have been exhausted by the high exploitation rates and low survival to maturity. Only the existence of refugia for reproductive lobster was thought to prevent collapses in many areas (Anthony and Caddy, 1980). To-date, only two hypotheses have been advanced for the recruitment pulse : 1) a large-scale climatic change; and 2) a decrease in fishing mortality during the 1970s. However, there has been no testing of postulated mechanisms. More recent studies have concentrated on larval transport problems (Hudon *et al.*, 1986; Harding and Trites, 1988, 1989) and the ecology of early benthic stages (Hudon, 1987; Hudon and Lamarche, 1989). The current debate centers partly on the behavioural ecology of the cryptic early benthic stages and possible density-dependent controls in local areas. Various mechanisms linking lobster larval settlement and subsequent recruitment into the fishery have been postulated (Aiken and Waddy, 1986). Several authors have stressed the importance of protective habitat availability for juveniles to lobster population dynamics (Cobb *et al.*, 1986; Fogarty and Idoine, 1986; Garnick, 1989). Thus, limited suitable bottom may be a 'bottleneck' that stabilises and strengthens the resilience of the fishable stock, but, also, limits recruitment into the fishery. A similar scenario has been advocated for settling larvae of Norway lobster, *Nephrops norvegicus* (Hill and White, 1990).

Fogarty and Idoine (1986) applied their arguments on shelter-mediated, density-dependent regulation of prerecruit lobster to ecological theory for animals with complex life cycles (Wilbur, 1980). American lobster may be considered K-selected strategists (life-history characterised by low fecundity, large egg size, parental investment in brooding eggs, repeat spawning in successive seasons, large body size, late sexual maturity, and longevity) which typically have low recruitment variability and are adapted for exploiting physically stable environments controlled largely by density-dependent

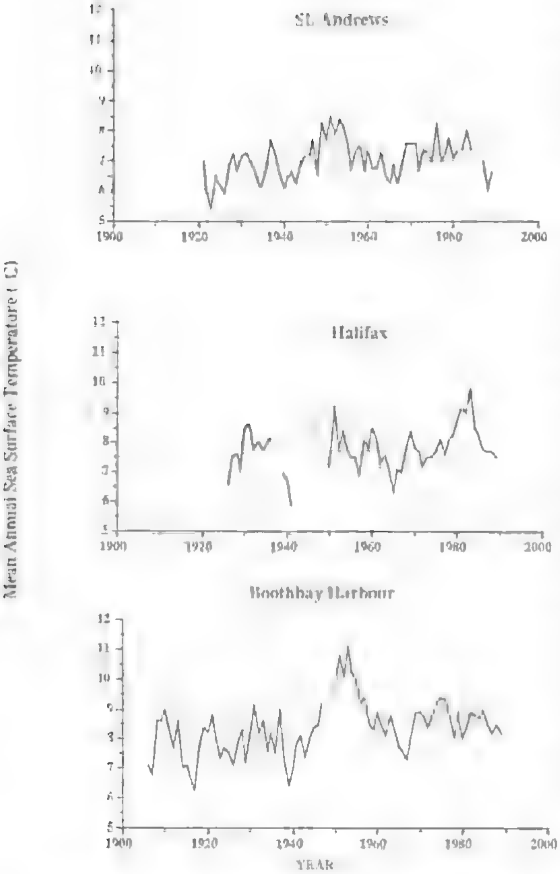

FIG. 4. Mean annual sea surface temperature profiles for St. Andrews, New Brunswick; Halifax, Nova Scotia; and Boothbay Harbor, Maine; note generally elevated values in late 1970s/ early 1980s.

forces (Barnes and Hughes, 1982). In contrast, other crustaceans such as shrimp with small bodies, rapid growth, early sexual maturity and high fecundity are opportunistic, r-selected, organisms adapted to physically unstable environments and subject to wide fluctuations in recruitment. Applying Wilbur's (1980), criteria, the American lobster could be classified by 'Density-Dependent Regulation Only During the Larval Stage'. Theoretically, the adult population varies with the productivity of the larval habitat (substitute early-stage, benthic, juveniles in the case of lobster), and if adults are long-lived, the age structure would reflect the relative 'larval' success of recent year classes. However, while such theory may have been suitable for guiding research on lobster recruitment mechanisms in the 1970s, the current improved recruitment trend is more reminiscent of an r-selected strategist, and accepted life-history theory appears to have little application. Rather, the scenario seems akin to the current 'supply-side' paradigm where recruitment levels can change internal controls normally operating within a system (Gaines and Roughgarden, 1985; Lewin, 1986; Underwood and Fairweather, 1989).

American lobster yields have always been geographically variable. Although landings improved in all fishing areas during the 1980s, yields from some increased far more than in the traditionally stable areas off Maine and Newfoundland (Fig. 3). Pezzack (in press) distinguished areas stable between 1947–1986, including Maine, Newfoundland, Grand Manan, southwestern Nova Scotia, the Gulf of St. Lawrence, Quebec, northeastern Cape Breton and Massachusetts. The areas which have exhibited wide fluctuations in landings are the eastern shore of Nova Scotia and southeastern Cape Breton. Lobster fishing grounds along the Atlantic-coast of Nova Scotia have displayed differing degrees of response to the improved recruitment of the 1980s (Fig. 5). Inter-ground stability differences could be due to differences in continental shelf area, which effect retention of larvae and substrate and food availability for juveniles, as well as physical environment.

DISCUSSION

Although a fundamental appreciation of the American lobster's life history was achieved early in this century with classic studies by Herrick (1896, 1911) and Hadley (1906, 1908) the subsequent history of research into stock-recruitment relationships has been somewhat *ad hoc*, apparently suffering from a lack of a concerted approach. Research thrusts seem to have changed opportunistically with ecological fads (Abrahamson *et al*., 1989) rather than doggedly addressing fundamental questions until they were solved. Work during the 1940s and 1950s focussed mainly on growth and movement of lobster that had already recruited into the fishery in an effort to prevent growth overfishing (Wilder, 1947, 1948, 1958). During the 1960s to mid-1970s there were various attempts both to identify stocks (Saila and Flowers, 1969; Barlow and Ridgeway, 1971; Cooper and Uzmann, 1971; Tracey *et al*., 1975) and to explain trends in landings through environmental influences such as temperature (Dow, 1961) and river discharge (Sutcliffe, 1973). Lobster research from the mid-1970s to early 1980s was influenced by

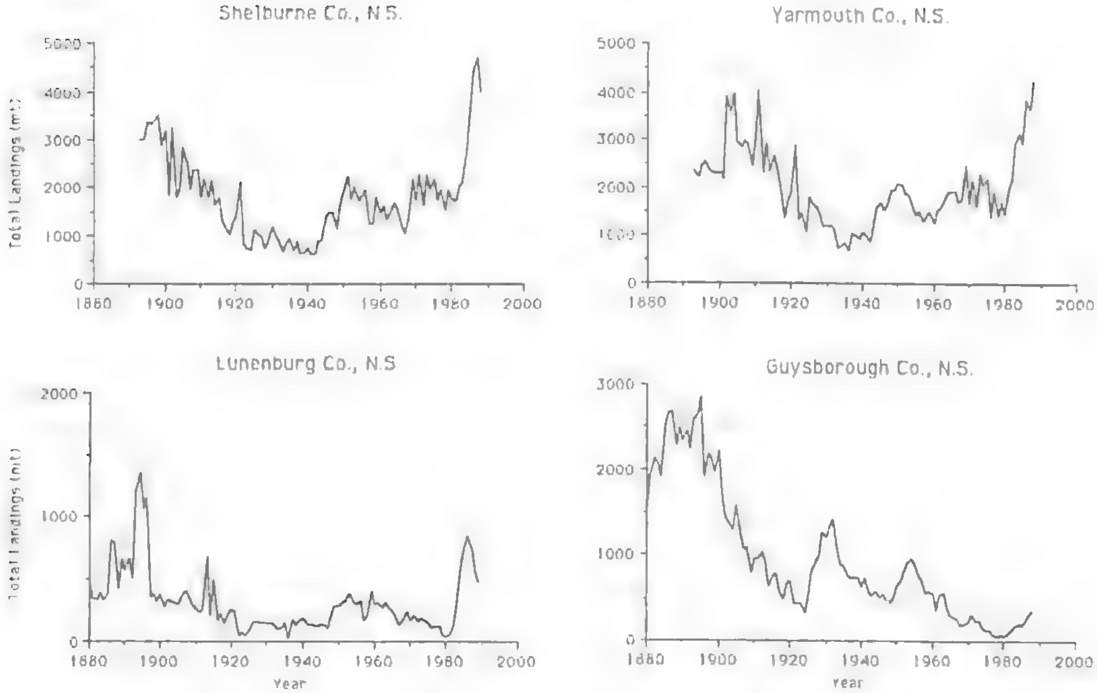

FIG. 5. Annual landings of American lobster for representative historically stable (Shelburne County, Yarmouth County) and collapsed (Lunenburg County, Guysborough County) fishing grounds along the Atlantic coast of Nova Scotia, to illustrate various degrees of response to the general increase in yield during the 1980s; for geographic areas that have remained more stable throughout see profiles for Maine and Newfoundland (Fig. 3).

vigorous arguments over the impact of the causeway across the Strait of Canso (McCracken, 1979) and the ecological implications of destructive grazing by sea urchins (Elner and Vadas, 1990). The controversy subsided without clear resolution as landings recovered, and the emphasis of research changed again. Recent investigations focus on larval transport and the movement of adult lobsters although work on the population ecology of early life-history stages has continued. While the numerous studies on *H. americanus* over the past century provide a valuable general understanding, they reach no consensus on the major factors influencing recruitment.

The recent recruitment pulse and major increase in landings in Canada started around 1981 and has unshackled both the Sutcliffe model correlating Quebec lobster landings and river run-off (Drinkwater *et al.*, in press) and stock discrimination based on historical landings patterns (Campbell and Mohn, 1983). We believe that the causitive mechanism(s) must be very powerful to have effected virtually all lobster fisheries. Landings increased more or less in unison throughout coastal Nova Scotia and the southern Gulf of St. Lawrence, but in varying degrees in local areas, suggesting that large environmental force(s) may have acted during the same general time period to influence recruitment. The various density-dependent mechanisms invoked as population controls of the cryptic early benthic stages of lobster in local areas are unlikely to account for large-scale recruitment events. Changes in climate coupled, perhaps, with decreased exploitation rates in the last 20 years are a more probable cause. We speculate that larval and early juvenile survival was enhanced during several years in the late 1970s-to-early-1980s through increased growth and food availability probably due to an increase in water temperature (Fig. 4). Also, low fishing mortality in some areas during the late 1970s could have allowed more females to produce eggs and the increased number of eggs per recruit may have swollen recruitment into the fishery 5–8 yr later (Campbell, 1990b). Subsequently differential individual growth rates spread this cohort into the fishery over several years, resulting in 3–5 years of record landings. Coupled with increased lobster abundance, fishing effort and total mortality of lobster increased dramatically in some areas (Campbell, 1990b).

'Supply-side' lobster recruitment controlled by an unpredictable climatic phenomenon has profound implications for fisheries management. Most management initiatives are based on the understanding that fishing mortality can have a strong impact on annual recruitment and that regulation of fishing pressure can preempt recruitment problems. If, as the events with lobster in the northwestern Atlantic over the past 10 years suggest, recruitment can be independent of fishing pressure then proactive management becomes essentially impotent, with managers only being able to react to changes in stock abundance as they occur. The situation would make recruitment predictions largely dependent on understanding and forecasting the causative environmental mechanism(s). Traditional fisheries models based on concepts such as surplus production and stable recruitment would be largely redundant.

While much is known about the biology of American lobster a conspicuous inability to understand recruitment remains compared to the successes achieved for the western rock lobster, *Panulirus cygnus* (Caputi and Brown, 1986; Phillips, 1986). Progress appears to have been hindere'd by three factors. First, the numerous attempts to develop a passive collector to intercept and index the recruitment strength of American lobster postlarvae at settlement have all failed. Instead, trial collector designs have succeeded in capturing early benthic stages of the commercial rock crab, *Cancer irroratus* (Beninger *et al.*, 1986). Second, comprehensive long-term data sets on oceanographic events (other than sea surface temperature and river discharge), prerequisites to exploratory correlation analysis and effective generation of hypotheses on physical controls on lobster recruitment, have not been available. Thirdly, the overall scientific approach appears to lack rigor. Although numerous explanations for recruitment patterns in American lobster have been advanced there has been little actual experimental testing of actual hypotheses and no concerted attempt to sequentially advance by 'strong inference' (Elner and Vadas, 1990). We believe that only by effectively addressing these three factors together can a realistic model of a biological lobster stock, integrating physical and oceanographic parameters with the complete life-cycle and ecology in a defined area through time, be achieved. Such a model of the whole system is required before the various system components can be viewed in context, their relative influences explored, and predictive models developed.

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